P. S. Prakasa RAO*: **Wood anatomy of some Combretaceae**

P. S. プラカサ・ラオ*: シクンシ科の材の構造

Our knowledge of the morphological features of the varied elements of the secondary xylem of the combretacean taxa is rather scanty and fragmentary (Coster, 1927; Panshin, 1932; Chowdhury, 1934, 1936; Helm, 1937; Metcalfe & Chalk, 1950). Further, heretofore, no systematic approach to the family on the basis of wood anatomy has been endeavoured. Keeping in mind these view-points the writer has embarked on the xylotomy of Combretaceae. The present communication concerns the morphological features of the axial elements of the secondary xylem in 39 species spreading over 15 genera as well their bearing on the status and interrelationships of the genera and tribes that comprise the family.

Materials and Methods The sources from which the different woods were procured and used in the study are given hereunder in the Table 1.

For the studies on the features of the secondary xylem, wood blocks were boiled and softened in hydrofluoric acid, washed, dehydrated and stored in a glycerine-alcohol mixture for further use. Transverse, tangential and radial sections were cut on a Jung wood microtome and stained using celestine blue-iron alum safranin formula of Gray and Pickle (1956). Macerations of wood of the above samples were accomplished, using the method of Wilson and Shutts (1957). The size classes of wood features are in agreement with the recommendations of Chattaway (1932), Chalk (1938) and the Committee on Standardization (1937). In describing the parenchyma recourse was made to the classification of Bailey and Howard (1941) and Carlquist (1962).

Observations The observations made pertain to the morphological features of the varied axial elements of the woods of the diverse members studied. Attention has been paid only to such features as recognised to be of avail in phylogenetic and taxonomic considerations (Tippo, 1941; Rodriguez, 1957; Carlquist, 1962). These comprise the general distribution of

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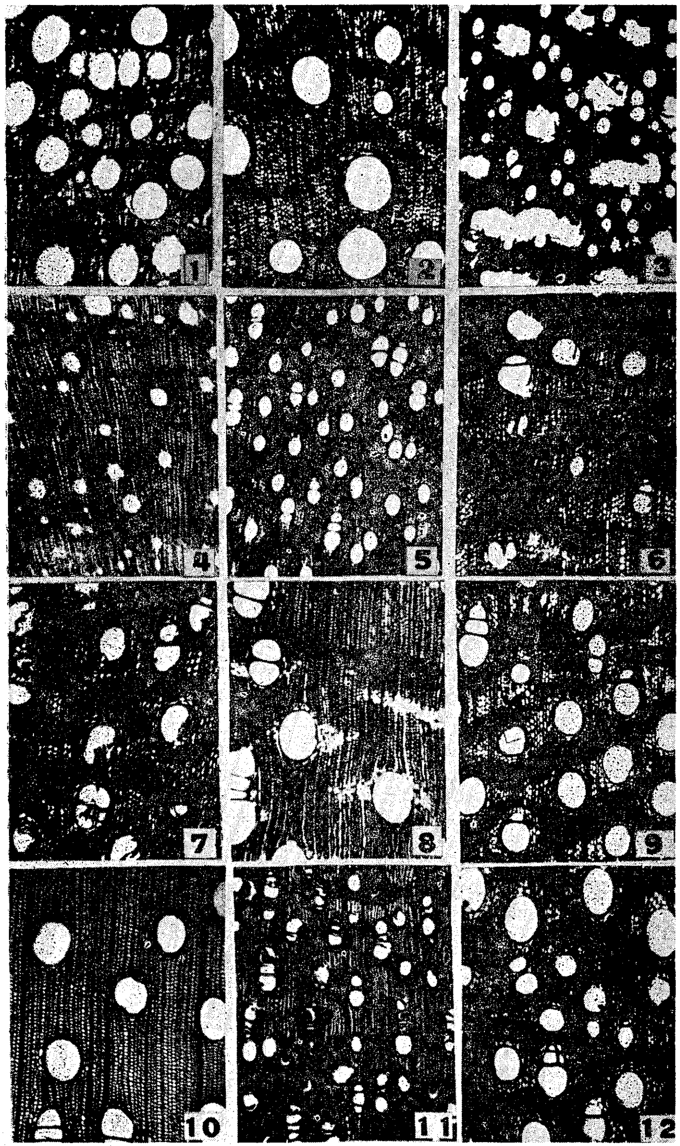
Table 1. Materials used for the present study.

Name of Plant	Name of Collector	Locality
Family: Combretaceae		
Subfamily: Combretoideae (of Exell, 1931)		
Tribe: Combreteae		
Combretum lamprocarpum Diels	L. Chalk	England
C. apetalum Wall.	〃	〃
C. aculeatum Vent.	〃	〃
C. sokodense Engl.	〃	〃
C. fruticosum (Loefl.) Stuntz.	G. Baylin	Connecticut, U. S. A.
C. molle R. Br. ex Don	L. Chalk	England
Quisqualis indica Linn.	P. N. Rao	Visakhapatnam, India.
Guiera senegalensis Lam.	Director, Forest Research.	Ibadan, Nigeria.
Poivrea coccinea DM.	B. S. M. Dutt.	Gudivada, India.
Pteleopsis myrtifolia (Laws) Engl. et Diels	G. L. Franklin	England
Tribe: Terminalieae		
Terminalia catappa Linn.	Author	Visakhapatnam, India.
T. bellerica Roxb.	〃	〃
T. chebula Retz.	〃	〃
T. paniculata Roth	〃	〃
T. arjuna W. et A.	〃	〃
T. procera	Mill Manager	Chatam, Andamans
T. bialata	〃	〃
T. myriocarpa Heurck et Muell.	W. R. Shuttie	Papua, New Guinea
T. microcarpa Decne.	〃	〃
T. rubiginosa K. Schum.	〃	〃
T. canaliculata Exell	〃	〃
T. complanata K. Schum.	〃	〃
T. copelandi Elmer.	〃	〃
T. phellocarpa King	L. Chalk	England
T. mollis Laws.	〃	〃

T. amazonia (Gmel.) Exell	L. Chalk	England
Bucida buceros Linn.	〃	〃
B. capitata	G. Baylis	Connecticut, U. S. A.
Buchenavia capitata (Vahl) Eichll.	G. L. Franklin	England
B. oxycarpa Eichll.	〃	〃
B. fanshawei	〃	〃
Anogeissus latifolia Linn.	Author	Araku, India.
Conocarpus erectus Linn.	G. L. Franklin	England
C. acuminata Linn.	L. Chalk	〃
Ramatuela argentea HBK.	G. L. Franklin	〃
Tribe: Calycopterideae		
Calycopteris floribunda Lamk.	R. S. Rao	Poona, India.
Tribe: Laguncularieae		
Lumnitzera racemosa Willd.	Director, Forest Research.	Laguna
Laguncularia racemosa Gaertn. f.	G. Baylis	Connecticut, U. S. A.
Macropteranthes fitzalani F. V. M.	L. Chalk	England

vessels, their diameter, length and inclination of their end walls; the nature and extent of pitting on them and their wall thickness. Likewise, attention has also been paid to more significant morphological features of fibres and axial parenchyma.

Figs. 1–12. 1: ***Combretum fruticosum***, cross-section of xylem showing pore distribution, diffuse porosity of the wood, pores in singles, fibrous elements and nature of axial parenchyma. 2: ***Quisqualis indica***, cross-section of xylem showing the pores in singles, fibrous elements and parenchyma. 3: ***Guiera senegalensis***, transverse section of xylem showing pores in singles and radial multiples, thick-walled fibres, scanty parenchyma and included phloem. 5: ***Pteleopsis myrtifolia***, cross-section of xylem displaying pores both in singles and radial multiples, thick-walled fibres and paratracheal parenchyma and some diffuse apotracheal parenchyma. 6: ***Terminalia arjuna***, xylem showing pores in singles and radial multiples, and parenchyma both apotracheal and paratracheal. 7: ***Terminalia paniculata***, cross-section of xylem dispalying pores in singles, radial multiples and aggregates, and parenchyma of different types. 8: ***Terminalia bialata***, cross-section of xylem showing the pores, fibrous elements and abundant axial parenchyma. 9: ***Terminalia myriocarpa***, cross-section of wood showing pores in singles and aggregates, paratracheal and apotracheal wood parenchyma. 10: ***Terminalia mollis***, transverse section of wood showing pores in arrangement, thin-walled fibres and meagre parenchyma. 11: ***Bucida buceros***, cross-section of wood showing pores in singles and radial multiples, abundant parenchyma and semilibriform fibres. 12: ***Buchenavia oxycarpa***, cross-section of xylem showing the pores, fibres and parenchyma.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The growth rings are evident to the naked eye only in *Terminalia arjuna, T. procera, T. bialata, T. myriocarpa, T. canaliculata, T. phellocarpa, Buchenavia capitata, Ramatuela argentea* and *Macropteranthes fitzalani.*

Vessel Element——All the woods are exclusively diffuse porous (Figs. 1–20) ; the pores being regularly distributed throughout the growth ring and very nearly of the same size. Solitary pores are most numerous and the pore clusters are least abundant (Table 2). The pore multiples range from 5 to 12% in the members of Combreteae, 8 to 32% in *Terminalia*, 21% in *Anogeissus latifolia*, 15 to 28% in *Buchenavia*, 21 to 26% in *Bucida*, 20 to 24% in *Conocarpus*, 15% in *Ramatuela*, 1% in *Calycopteris*, and 5 to 15% in members of the Laguncularieae. Pores in aggregates are very occasionally recorded in *Terminalia catappa, T. arjuna, T. bellerica, T. chebula, T. myriocarpa, Bucida, Conocarpus, Ramatuela argentea, Lumnitzera racemosa* and *Laguncularia racemosa*. Pore chains are totally lacking in the members, although the distribution of pores in *Macropteranthes fitzalani* simulates pore-chain condition (Fig. 20). The number of vessels per square millimeter is numerous in all species studied excepting some like *Lumnitzera, Laguncularia* and *Macropteranthes* in which they conform to the category of most numerous (Table 2).

The cross-sectional diameters range from very small to very large (30–325 μ) and similarly their length measures from 80 to 960 μ (short to moderately large : Table 2) in the members presently studied. The vessel

Figs. 13-24. 13: *Buchenavia capitata*, secondary xylem displaying in cross-section of the pores, thick-walled fibrous elements and abundant parenchyma. 14: *Anogeissus latifolia*, cross-section of wood showing the arrangement of the pores, thick-walled fibres and parenchyma. 15: *Conocarpus accuminata*, transverse section of wood showing diffuse porosity, thick fibres and paratracheal and scanty apotracheal parenchyma. 16: *Ramatuela argentea*, cross-section of wood showing diffuse porous condition, fibres and abundant parenchyma. 17: *Calycopteris floribunda*, secondary xylem in transverse section showing diffuse porous nature, parenchyma and included phloem. 18: *Lumnitzera racemosa*, wood in transection showing the pores in singles and radial multiples, semilibriform fibres and parenchyma. 19: *Laguncularia racemosa*, wood in transverse section showing pores in abundant number, confluent parenchyma, thick-walled fibres. 20: *Macropteranthes fitzalani*, wood in transverse section showing diffuse porous condition, large number of minute pores, scanty parenchyma and thick-walled fibrous elements. 21: *Combretum sokodense*, wood in tangential section showing thick-walled nonseptate fibres, vessel end walls and uniseriate rays. 22: *Terminalia canaliculata*, wood longitudinal section showing thin-walled nonseptate fibres and uni- and tri-seriate rays. 23: *Anogeissus latifolia*, wood in longisection showing semi-libriform septate and nonseptate fibres, vessel end walls and uniseriate rays. 24: *Lumnitzera racemosa*, wood in tangential section showing intervascular pits, septate and non-septate fibres and exclusively uniseriate rays.

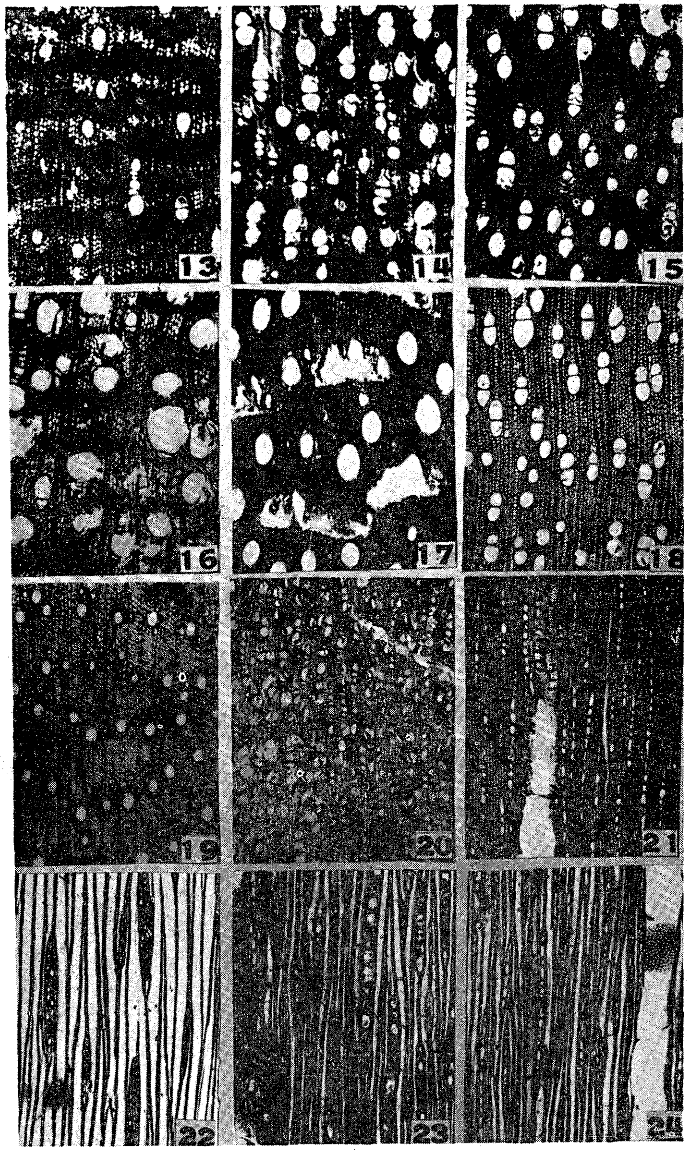
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Table 2. Pertinent morphological features of the vertical elements of the secondary xylem of species, in the Combretaceae investigated in the present study (+=present; −=absent).

Species	Pore distribution (in mm²)	Pore arrangement (%)			Vessel element diameter (μ)	Vessel element length (μ)	Vessel element endwall inclination (°)	Fibre length (μ)	Fibre wall thickness (μ)	Parenchyma	
		Singles	Radial multiples	Aggregates						Paratracheal	Apotracheal
Combretum lamprocarpum	40–45	95	5	−	75–200	160–272	30–85	384–1152	7–12	+	+
C. apetalum	40–45	95	5	−	30–120	240–400	30–85	240– 880	8–12	+	+
C. aculeatum	40–42	95	5	−	30– 90	140–320	30–85	352–1040	8–12	−	+
C. sokodense	40–65	95	5	−	48–142	240–304	30–85	350–1100	8–11	+	+
C. fruticosum	30–36	95	5	−	30–180	80–352	30–85	512–1312	7–12	+	+
C. molle	35–40	95	5	−	30–120	114–336	30–80	448–1440	8–10	+	+
Quisqualis indica	30–45	95	5	−	50–180	288–480	50–70	896–1260	4– 7	+	−
Guiera senegalensis	30–45	95	5	−	45– 95	152–400	50–65	272– 400	8–10	+	−
Poivrea coccinea	75–90	95	5	−	36–110	240–400	40–70	240– 880	6– 8	+	+
Pteleopsis myrtifolia	30–45	88	12	−	35– 90	400–960	40–65	1152–2000	7–10	+	+
Terminalia catappa	15–17	74	26	−	60–300	160–480	60–87	375–1460	4– 5	+	−
T. arjuna	8–10	69	31	−	120–245	80–500	50–70	370–1600	4– 5	+	+
T. bellerica	8–10	74	26	−	150–325	170–680	65–75	400–1985	4– 5	+	+
T. chebula	9–17	68	32	−	120–215	160–600	50–80	350– 785	4– 5	+	+
T. paniculata	11–13	83	14	3	115–250	180–600	65–75	700–2000	5– 6	+	+
T. procera	9–11	85	12	3	150–320	240–432	60–75	896–1680	5– 6	+	+

T. bialata	10–12	76	22	2	120–300	260–480	60–75	512–1600	4– 5	+	−
T. myriocarpa	10–12	80	20	—	180–325	112–336	50–70	600–1150	3– 4	+	+
T. microcarpa	10–17	85	13	2	45–215	240–550	50–75	600–1150	3– 4	+	−
T. rubiginosa	16–18	85	13	2	110–221	110–810	65–75	550–1200	4– 5	+	−
T. canaliculata	12–15	82	15	3	120–230	300–600	60–75	600–1200	3– 4	+	+
T. complanata	11–18	80	18	2	60–190	250–600	62–82	600–1500	3– 4	+	−
T. copelandi	22–30	92	8	—	160–210	180–680	70–85	660–1320	4– 5	+	−
T. phellocarpa	20–22	75	20	5	120–230	240–480	60–75	672–1504	4– 5	+	−
T. mollis	18–21	70	25	5	45–252	80–288	45–85	416–1520	3– 5	+	−
T. amazonia	17–20	78	20	2	80–288	120–290	40–70	400–1120	4– 5	+	−
Bucida buceros	11–22	79	21	—	62– 80	344–560	56–72	560–1360	7– 8	+	−
B. capitata	11–22	74	26	—	62– 90	260–460	50–78	350–1260	7– 8	+	−
Buchenavia oxycarpa	22–30	70	28	2	60–225	320–560	40–75	448–1402	7– 8	+	+
B. capitata	22–75	80	15	5	48– 64	192–720	60–85	1040–1872	6– 8	+	+
B. fanshawei	22–27	78	20	2	70–250	224–512	50–75	1008–1840	6– 8	+	+
Anogeissus latifolia	22–45	76	21	3	65– 90	100–575	50–85	370–1800	5– 6	+	+
Conocarpus erectus	65–75	76	24	—	50– 80	320–422	65–82	880–1280	6– 8	+	+
C. acuminata	69–72	80	20	—	60– 80	360–480	70–88	720–1460	7– 8	+	+
Ramatuela argentea	40–45	85	15	—	90–220	400–760	60–85	400–1200	8– 9	+	+
Calycopteris floribunda	50–75	99	1	—	60–230	200–400	55–85	520– 824	4– 8	+	+
Lumnitzera racemosa	230–260	95	5	—	32–110	120–480	45–65	450–1200	3– 6	+	−
Laguncularia racemosa	200–220	91	9	—	60–120	320–580	60–85	960–1392	6– 7	+	−
Macropteranthes fitzalani	330–400	85	15	—	35–120	278–576	60–75	432–1088	7– 8	+	−

walls are unevenly thickened and among the species the thickness varies from 4 to 8 μ.

Intervascular pitting is profuse and typically alternate, bordered and vestured (Fig. 24). Pits to parenchyma and rays similar: bordered-alternate.

The perforation plates are exclusively simple and they are either circular or oval. The angles of the end-walls are oblique to nearly horizontal and range from 30°–88° in the varied species presently investigated (Figs. 21 to 24).

Fibrous Element——The ground mass of the wood is composed mostly of fibres in the members studied, though the occurrence of a very low percentage of fibre-tracheids is restricted to *Terminalia mollis, Lumnitzera racemosa, Laguncularia racemosa* and *Macropteranthes.* Fibres are for the most part non-septate (Fig. 22). However, a low percentage of septate fibres do occur in certain species like *Pteleopsis myrtifolia, Poivrea coccinea, Terminalia catappa, T. arjuna, T. paniculata, T. procera, T. bialata, T. myriocarpa, T. amazonia, Anogeissus latifolia, Conocarpus erectus, C. acuminata, Lumnitzera racemosa* and *Laguncularia racemosa* (Fig. 24). None of the species exhibited gelatinous fibres. The length and the wall thickness of the fibrous elements show variation as in vessel elements by species worked out. For the most part the fibres are short to medium-sized (240–2000 μ) and their walls are thin to thick in all the genera excepting *Bucida, Buchenavia,* certain species of *Terminalia, Anogeissus, Ramatuela* and *Micropteranthes* (Figs. 3, 5 to 7, 11 to 17 and 20) in which the walls are very thick.

Parenchyma——The parenchyma is predominantly paratracheal. In certain members, namely, *Combretum, Poivrea, Pteleopsis, Terminalia, Buchenavia, Anogeissus, Conocarpus, Ramatuela* and *Calycopteris* there is a tendency to the formation of apotracheal parenchyma besides abundant occurrence of paratracheal parenchyma (Figs. 1, 4, 6, 7 to 9, 12, 13, and 15 to 17). Among the memebrs studied only a few species manifest very scanty parenchyma in their wood (Fig. 10). Many minute simple pits are found on the walls of the axial parenchyma cells.

The anatomical data pertaining to the vertical elements for the species studied is presented in the Table 2.

Discussion and Conclusions The anatomical features of 39 species belonging to 15 genera of Combretaceae are described in the present study.

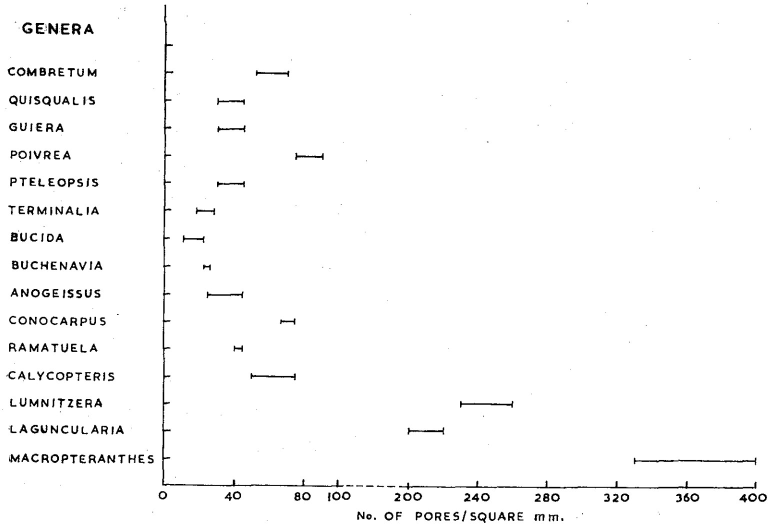

Fig. 25. The ranges between the minimal and maximal values of the numbers of pores per mm² in the Combretaceae.

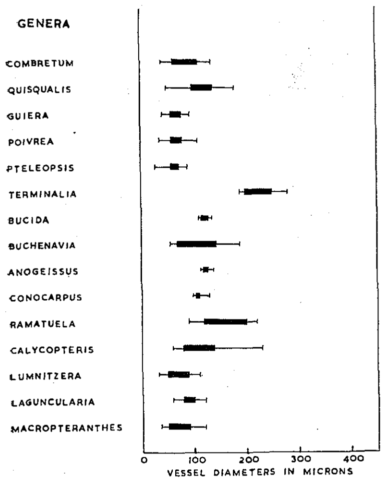

Fig. 26. The ranges between the minimal and maximal values (——) and the most frequent ranges (▬) in the cross-sectional diameters of vessel elements in the Combretaceae.

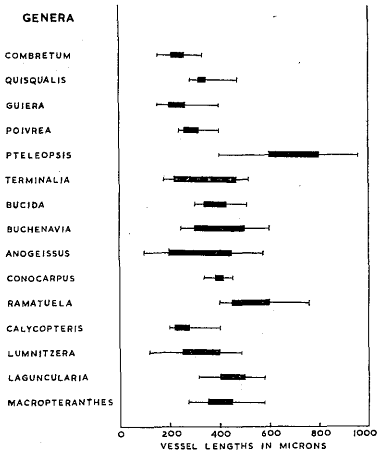

Fig. 27. The ranges between the minimal and maximal values (——) and the most frequent ranges (▬) in the length of vessel elements in the Combretaceae.

In order to evaluate the probable evolutionary status of the different members or the tribes on the basis of wood anatomy, it would be more appropriate to consider the salient anatomical features of proven taxonomic importance of each of the tribes and thus obtain a comprehensive view of the Combretaceae as a whole. To facilitate such a consideration, a comparative account of each of the individual anatomical features presently studied are summarized in the figures (25–29). A critical analysis of the data brings out certain interesting features which are outlined hereunder:

In the distribution of the vessel elements (Table 2 and Fig. 25) the members of the Laguncularieae manifest maximum number per square millimeter. Of the three genera of this tribe examined, the number ranges from 330 to 400 per square millimeter in *Macropteranthes* followed by the two other genera, *Lumnitzera* and *Laguncularia*. Among the Terminalieae the maximum number of vessels is recorded for *Conocarpus* followed by *Ramatuela*, *Anogeissus*, *Buchenavia*, *Terminalia* and *Bucida*. The genera *Poivrea* and *Combretum* of the Combreteae and to some extent *Calycopteris* of Calycopterideae seem to be nearer to *Conocarpus* in this feature, since in all these members the average number of vessels per square millimeter varies around 70. The genus *Poivrea*, however, shows maximum number of vessels among all the members examined with the exception of those of Laguncularieae. Genera like *Quisqualis*, *Guiera* and *Pteleopsis* of Combreteae may be considered to be in some degree nearer to the members like *Anogeissus* or *Ramatuela* of Terminalieae.

Although the vessel abundance is a criterion not yet established to have phylogenetic importance (Carlquist, 1962), we may expect some sort of inverse correlation between the vessel number and their cross-sectional diameters as these features together are governed to some extent by the special relationship of not only vessels but even the preponderance of other constituent tissues of the secondary xylem. Accordingly, the Laguncularieae which show the maximum abundance have vessels which are relatively narrow when compared with those of Combreteae, Terminalieae and Calycopterideae. In other words, on the basis of the vessel diameters Laguncularieae may be considered as most primitive and *Terminalia* of Terminalieae as the most advanced among the Combretaceae. Such an inference on the evolutionary status of the Laguncularieae and the Terminalieae

received support indirectly from the respective vessel diameters observed in them (Fig. 26). It is recognised that significantly larger pores are more evolved than those that are small (Rodriguez, 1957).

While the inverse correlation between vessel abundance and their diameters may be obvious in the case of Laguncularieae and Terminalieae, such a correlation may not be apparent in all the cases. Majority of the genera have vessels with diameter ranging approximately between 35 and 142 μ (Fig. 26). Only five genera namely *Quisqualis, Terminalia, Buchenavia, Ramatuela* and *Calycopteris* have pores with relatively larger diameters compared with the rest of the Combretaceae. Assuming that the presence of vessels with large diameters is an advanced feature as suggested by Rodriguez (1957), *Terminalia, Buchenavia, Ramatuela* and *Calycopteris* are most highly advanced. The Combreteae seem to be somewhat similar to the Laguncularieae in their evolutionary status on the basis of vessel diameters. The genera *Bucida, Anogeissus* and *Conocarpus* differ from the rest of the Terminalieae as they have vessels smaller than those of the Laguncularieae. Thus on the basis of this feature, *Bucida, Anogeissus* and *Cono-*

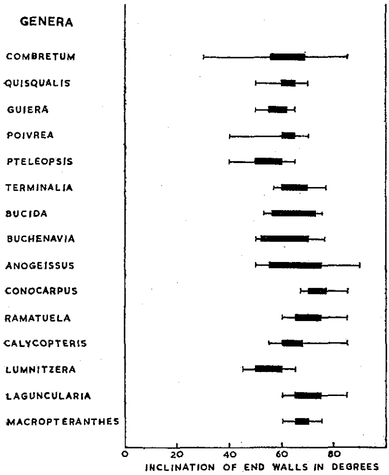

Fig. 28. The ranges between the minimal and maximal values (——) and the most frequent ranges (▬▬) of the inclination of the end walls of vessel elements in the Combretaceae.

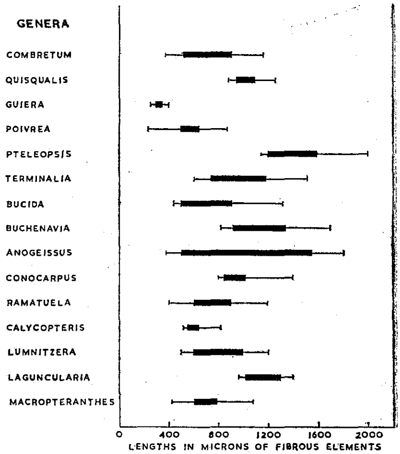

Fig. 29. The ranges between the minimal and maximal values (——) and the most frequent ranges (▬▬) of the lengths of fibrous elements in the Combretaceae.

carpus are as primitive as the three genera of Laguncularieae are. The genera *Buchenavia* and *Calycopteris* seem to occupy an intermediate position between the extremes exhibited by Terminalieae and the Laguncularieae.

While it was possible to make some positive inference on the basis of vessel diameters, the data collected on the vessel lengths do not seem to yield any valuable information of the evolutionary trends among the Combretaceae. An analysis of the data given in Fig. 27 reveals that generally speaking the members of the Combreteae and *Calycopteris* possess the shortest vessels, which represent an evolved condition among the Combretaceae. On the other hand, *Pteleopsis* possessing relatively long vessels among the Combreteae represent a low evolutionary status. The rest of the members of Combreteae, including those of the Laguncularieae, apparently represents intermediate condition. Although the vessel lengths are useful in the phylogenetic considerations (Rodriguez, 1957), it is established by Stern and Greene (1958) that stabilisation in the lengths of these elements is extremely slow and that unless one has access to such material the importance of this criterion in phylogenetic considerations is very much reduced. Therefore, the vessels in the process of development are likely to show considerable variations due to which the size character does not offer reliable criterion. The somewhat contradictory indications exhibited by the vessel lengths of the Combretaceae presently studied are probably suggestive of such a situation.

Although the different members examined show certain variations in some of the features of their vessels as discussed above, in certain other features which are also recognised to be of taxonomic avail they show some uniformity. For example, the angle of inclination of the vessel end walls mostly ranges between 50° and 75° as can be seen from Fig. 28. In this feature all the members of the Combretaceae may be regarded as showing a moderately advanced condition as in none of them the end walls show a sharp angle of inclination, which is reckoned as a primitive feature (Frost, 1931). Similarly the intervascular pitting is alternate in all the species studied. It has been recognized that the evolutionary line of the intervascular pitting on the side walls of vessels is from scalariform to transitional and then to opposite and finally alternate (Frost, 1931). As such, the consistency, with which the above described pits occur in all the Combretaceae,

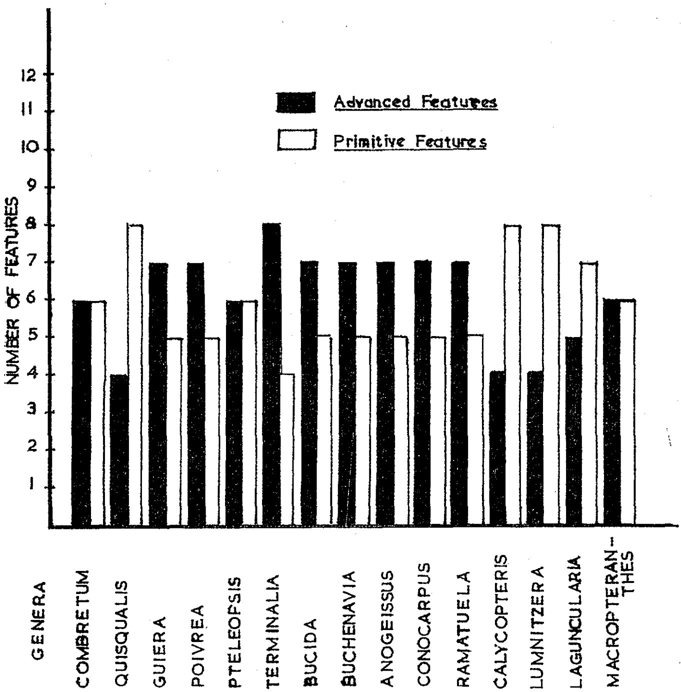

Fig. 30. Comparison of anatomical features in genera of the Combretaceae in number.

indicates a relatively high evolutionary status of the family as a whole. One other feature suggestive of similar evolved condition in the organization of the vessel element is that they are mostly circular or oval in their cross-sectional views, whereas the angular appearance is considered to be a primitive feature (Rodriguez, 1957).

While the features such as the nature of pitting and the cross-sectional diameters of the vessel elements support an advanced status for the family, the occurrence of solitary pores in majority of members is suggestive of its primitiveness. The only few exceptions to this general feature are the members like *Pteleopsis* of Combreteae and *Lumnitzera* and *Macropteranthes* of Laguncularieae. In these three genera, radial multiples occur to an extent of 12%, 9% and 15% respectively. Terminalieae, however, do not seem to be comparable to the rest of the Combretaceae in this respect, in that the

radial multiples occur up to 32%. Similarly, a feature not shared by any Combretaceae, other than Terminalieae is the occurrence of vessel aggregates in members like *Buchenavia*, *Anogeissus*, and *Terminalia* though to a meagre extent. Therefore, on the basis of these two criteria, namely, the occurrence of radial multiples to a higher extent and the presence of aggregates to some extent, the Terminalieae are to be regarded as exhibiting a more advanced condition (Tippo, 1941) than the rest of the Combretaceae.

One more feature of taxonomic importance in respect of the vessel element is wall thickness. Moseley (1948) termed the vessels with walls less than 6 μ as thin-walled and those with more than 6 μ as thick walled and considered the former more advaneced than the latter. Applying the same criterion with respect to the Combretaceae, most of the members fall under the species with thick-walled vessel elements. Therefore, the family seems to be more specialized in this regard.

The morphological features of the fibrous elements occurring in the woods of various genera examined are summarized in the Table 2. It can be seen that the fibrous elements are either very short or moderately large in their lengths as assessed on the basis of size classes recognised by the Committee on the Standardization of Terms of Cell Size of the International Association of Wood Anatomists (1937). Extreme fibre lengths are recorded for *Pteleopsis*, *Buchenavia*, *Anogeissus* and *Terminalia* among the members examined (Fig. 29). Most of these fibres are nonseptate, excepting cases in *Combretum*, *Poivrea*, *Pteleopsis*, *Terminalia*, *Conocarpus*, *Anogeissus*, *Calycopteris*, *Lumnitzera* and *Laguncularia* in which the septate fibres are also present in a low percentage. In the total absence of short fibres, which may be described as such, and in the significantly low representation of the septate fibres if present in some members, the Combretaceae do not exhibit specialization in this feature. This suggests a low status of the Combretaceae. However, a feature of some significance in so far as the fibrous elements are concerned is that in majority of the genera the wall thickness, exceeding 6 μ, may be described as thick. Such a feature is considered as representing advanced state (Moseley, 1948). Only in some samples of the genera like *Quisqualis*, *Terminalia*, *Anogeissus*, *Calycopteris* and *Lumnitzera* the walls do show thickness less than 6 μ thus coming into the category of thin-walled fibres (Moseley, 1948). When fibrous elements alone are consid-

ered, therefore, both advanced (thick walls) and primitive (absence of short and septate fibres) conditions are known among the combretacean taxa.

In most genera the parenchyma is predominantly paratracheal. However, in some genera like *Combretum, Poivrea, Pteleopsis, Terminalia, Buchenavia, Anogeissus, Ramatuela* and *Calycopteris* a tendency for an apotracheal nature of the axial parenchyma is also encountered. In view of the meagre representation of the apotracheal parenchyma that too at a significantly low level, if present, the combretacean woods may be generally described as far as studied, as be typically paratracheal and may be considered to show a feature of some advancement (Carlquist, 1962). However, in genera like *Buchenavia, Laguncularia, Combretum* and *Terminalia* confluent type does occur along with the vasicentric paratracheal parenchyma. In majority of the genera the paratracheal parenchyma is both vasicentric and aliform. In some members aliform confluent type of parenchyma (Figs. 2, 7, 11, 13, 16, 19) is also encountered along with the two other types mentioned above. An interesting deviation from this basic pattern is the occurrence of scanty parenchyma, which is regarded as the most primitive condition recorded in some species of *Terminalia* (Fig. 10), *Lumnitzera* (Fig. 18) and *Macropteranthes* (Fig. 20). The total absence of scanty parenchyma in *Laguncularia* seems to be somewhat significant. Among the members exhibiting the apotracheal condition, the parenchyma is both diffuse and terminal in *Combretum, Pteleopsis* and *Terminalia*. In *Buchenavia* the apotracheal parenchyma is mostly initial, though there is a tendency approaching to the diffuse condition. Initial parenchyma is also encountered in *Calycopteris*.

A critical survey of the nature of the parenchyma mentioned above indicates an admixture of both primitive and evolved conditions to varying degrees in genera of the Combretaceae. It seems as though the differentiation of the axial parenchyma has not reached its culmination in combretacean taxa as is to be inferred from the occurrence of many intermediate stage in mature parenchyma. Thus the parenchyma of any one genus cannot be classed as strictly belonging to a distinct category representative of a determinate evolutionary status. It is likely that the members like *Combretum, Pteleopsis, Terminalia, Buchenavia* and *Anogeissus* displaying the more evolved features within the apotracheal parenchyma tend to establish the paratracheal parenchyma. In fact in all these taxa paratracheal paren-

chyma is also present and it may be suggestive of a transitional stage in the evolution of the latter from the former. In view of the rather complex nature of the wood parenchyma observed in the combretacean members, it may be reasoned, that the evolution of parenchyma in these woods is still in process of differentiation and that this element has not yet fully established in any definite pattern. It may also be inferred that the evolution in the nature of parenchyma has been in progress independent of other tissues that go to constitute the wood of combretacean member.

From the foregoing discussion it is obvious that there are many anatomical features in which the taxa show uniformity and that all of them have attained possibly the same degree of anatomical specialization, likely by parallel evolution, though independent each other. This is also in agreement with an advanced status suggested for the family on the basis of the occurrence of free nuclear endosperm (Venkateswarlu & Prakasa Rao, unpublished). This feature, when taken together with the occurrence of simple perforations of their vessel elements, gains additional significance (Swamy & Ganapathy, 1957). Likewise on the basis of floral anatomy (Venkateswarlu & Prakasa Rao, 1970) also it has been convinsingly proven that there is ample evidence to suggest a general reduction amongst the different genera of the Combretaceae. However, an intepretation as to the phyletic placement of the different tribes or genera within the family, relying solely on the xylotomical features, appears to be somewhat hazardous to formulate, for the reason that the family comprises members displaying an assemblage of features which signify both primitiveness and moderate phyletic advancement (Fig. 30). Nonetheless, the definite conclusions that could be made are that the diverse members, though constituting a composite group of closely related taxa, have evolved independently each other so as to reach the varying levels of specialization with respect to any one or more of the individual constituents of the secondary xylem and that Laguncularieae are distinct from the rest (Calycopterideae, Combreteae and Terminalieae) in the family. It has been indicated that Laguncularieae being characterised by significantly high number of vessels per unit area, their smaller cross-sectional diameters as well as their more sharply inclined end walls represent a low state of specialization. The three-traced sepals, vascularised annular disc and the maximum number of carpels met in *Lumni-*

tzera corroborate their least evolved condition compared to the rest of the Combretaceae (Venkateswarlu & Prakasa Rao, 1970). This gains further support on exomorphic features; Laguncularieae can be considered as the least evolved because of the pentamerous perianth in contrast to tetramerous Combreteae on the one hand and apetalous Calycopterideae and Terminalieae on the other. Further the analysis of xylotomical features of combretacean taxa merit the retention of the tribes of the subfamily Combretoideae of Exell (1931). The subfamily Strephonemotoideae of Engler and Diels (1889) and Exell (1931) is now removed and raised to the family rank, the Strephonemataceae (Venkateswarlu & Prakasa Rao, 1971) on the basis of wood characteristics; this family being closely allied to the Combretaceae.

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Summary

The morphological features of the vertical elements of the woods of 39 species belonging to 15 genera of the Combretaceae were studied and described.

An analysis of these data has revealed that all the members examined share certain common characteristics, such as diffuse-porosity, simple perforation plates, predominantly alternate intervascular pitting, semilibriform to libriform fibrous elements and paratracheal axial parenchyma. At the same time it is visualized that the different members display some amount of differences, when their wood features are comparatively analysed. Some of these features are: pore distribution, cross-sectional diameter and length of vessel elements, their end wall inclinations, the range of the occurrence and length of fibrous elements and the mode of distribution of wood parenchyma. The bearing of these variations, which signify both primitiveness

and moderate phyletic advancement of the different tribes (Laguncularieae, Calycopterideae, Combreteae and Terminalieae) that constitute the family (sensu str.), has been considered to some extent. Broadly speaking, it appears as though the different members of the Combretaceae, though constituting a composite group, have evolved independently each other so as to reach varying levels of specialization with respect to any one or more of the individual constituents. On an evolutionary basis, it is visualized that Laguncularieae are least specialized, Terminalieae most evolved and Calycopterideae and Combreteae occupying intermediate position within the family.

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シクンシ科に属する15属39種の材の解剖学的特徴について調査し，そのいくつかは科全体に共通であるが，膜孔の分布，導管横断面直径，終端細胞膜の傾斜度，繊維細胞の存否とその長さ，および柔組織の状態と分布には相違が見られることを明らかにした。また，これらの木部の解剖学上の形態の相違に基づいて，科内の系統についても論じた。

□水島正美博士 (1925–1972) Dr. Masami MIZUSHIMA (1925–1972)

本誌の編集員 水島正美博士は去る9月9日癌のため亡くなられた。大正14年4月14日府中市の生れで享年47才。

氏は大学卒業の頃にはすでに日本特に北地の植物に精通し広い智識をもっており，その研究態度は終始一貫して誠に真面目なものであった。論文を書く時に少しでも疑問の点があれば外国から標本を借用してでもこれを自ら確認し，一篇の参考文献をも見逃さない慎重さであった。野外にもよくでかけその観察は精細であり，採集した標本には生育状態，草丈，葉の光沢，花の色香など生時の観察が丹念に書き加えられていて今後多くの研究者に役立つことであろう。ナデシコ科植物を専攻し，昭和36年東京大学から理学博士の学位をうけ，特にツメクサ属 (1960)，ハコベ属 (1965)，ワチガイソウ属 (1965) などについて詳しい研究を発表した。それらの論文の引用文献，記載，分布などの一行一行にその注意深さがよくうかがわれ氏の性格を物語っている。また各地の植物調査に参加し，伊豆大島 (1951)，尾瀬地方 (1954)，伊豆青ヶ島 (1955–7)，長野県下水内郡 (1956)，下北半島 (1956–8)，木曾御岳 (1958)，山形県朝日岳 (1964) などのフローラをまとめた。

氏の略歴を記すと，昭和19年9月北海道大学予科農類を修了後同10月一旦北海道大学農学部水産学科に入学したが，若い時から植物を愛好し宮部金吾先生にすすめられて昭和21年5月東京大学理学部植物学科に入学，昭和24年3月に卒業，更に同年4月大学院に進み，29年3月修了して同年4月から資源科学研究所の研究員になった。